

Wyman (Jeff.) with the original
J. Wyman

ART. XXVI.—*Observations on the Development of ANABLEPS*
GRONOVII, (*Cuv. & Val.*) By JEFFRIES WYMAN, M. D.
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WHILE the general plan of the development of Fishes and Batrachian Reptiles conforms strictly to the an-allantoidian type, the external conditions under which the process of the formation of the embryo is carried on, vary to a very remarkable degree. In the larger majority of instances, eggs are scattered without care, or perhaps only a locality is selected which furnishes the most favorable circumstances, in relation to currents of water, the kind of bottom, the exposure to light, &c. Once deposited, they are no longer attended to.

In other cases, but these are comparatively few, the fishes construct something which serves to protect the eggs, and in a measure answers the purpose of a nest; in this the eggs are laid and undergo their evolution. The Lamprey builds a rude structure, consisting of a pile of stones brought from a distance, in the mouth; both sexes coöperating in the labor of building. The eggs are deposited between the stones as the structure is reared, and remain there in security until hatched. The Chub (*Catostomus tuberculatus*) has a similar habit. Our common Bream (*Pomotis vulgaris*,) and a species of *Gobius* found in the Mediterranean, (the *Phycis* of Aristotle,)* both construct a true nest, composed of aquatic plants, in which the ova are developed, one or the other of the parents standing guard as the embryo passes through its different stages. But the most remarkable nests built by fishes, are those of the "Hassars" (*Collicthys*) of Demarara, and of the "Sticklebacks" (*Gasterostei*) of Europe. The "Round-headed Hassar" forms its nest of leaves, and the "Flat-headed Hassar" of grass. Of the two species of Stickleback described by Coste,†

* Owen. Lects. on Comp. Anat. Vol. II. p. 304.

† Instructions Pratiques sur la Pisciculture, suivies de Mémoires, et de Rapports sur la même sujet. Par M. Coste, Professeur au Collège de France. Paris, 1852.

one forms a nest upon the bottom with pieces of grass and other vegetable substances, which are woven together, forming a covered structure, with two openings, so that when the fish enters it can pass through without being required to turn round to come out. If the materials prove too light, and show a tendency to float, they are loaded with stones till the nest is securely anchored.*

The other species constructs its abode upon some aquatic plant elevated above the bottom, or upon some submerged branch or twig of a tree. During incubation, the ova are guarded by the male, and protected against the depredations of the females, which are always ready to devour the eggs almost as soon as deposited.†

In another group of fishes, the eggs are neither scattered upon the bottom nor deposited in nests, but assume a more intimate relation with the parent, though still conforming to the oviparous mode. In the Pipe fishes they are attached to the body of one of the parents. In one species, *Syngnathus ophiodon*, the eggs merely adhere to the under side of the abdomen of the male, where they remain till hatched. But in *S. acus*, as observed by Ekströem and others, and in *S. Peckii*, as observed by Storer and myself, there is found a true marsupial pouch, consisting of two folds of skin, posterior to the anal opening of the male. These folds are directed inwards, and meet on the median line. In this pouch the eggs are deposited by the female, and remain there till incubation is complete, and even after the eggs are hatched the young return to the pouch as a place of refuge.

In all of the preceding instances the foetus is developed exterior to or upon the surface of the body. The Pipe-fishes, which are analogous to the Marsupials among Mammals, form

* For a very interesting account of the nest-building of the Sticklebacks, see Hancock Ann. & Mag. of Nat. Hist. Vol. X. N. S. p. 241.

† I have witnessed this habit in a pregnant female which was in my possession. The eggs were deposited during the night, but on the following morning nothing remained of their contents, the empty envelopes being scattered about the bottom of the vessel.

a transition to the next division, where the conditions of development are wholly changed.

Extended observations have proved, that a large number of species of fishes, belonging to many genera, are truly viviparous, the foetus passing through a real gestation by the parent before its development is complete. These Viviparous fishes may be divided into two groups, according to the position occupied by the embryo during the period of its growth.

I. In the first group may be arranged those fishes in which *the ova leaves the ovary in an undeveloped state, and in which the process of evolution is not commenced until it reaches the lower portion of the oviduct.* The species which this group comprises are nearly all, if not all, Plagiostomes. The best known are *Spinax*, *Carcharias*, *Mustellus*, *Galeus*, and *Torpedo*. Although they are usually classified among the lowest of fishes, it is in some of them that the process of reproduction becomes most nearly analogous to that of the highest Vertebrates. Not only does the yolk reach proportions like those of the yolk of birds, but the yolk-sac itself plays the part of an allantois, and forms an organ analogous to a placenta. In *Spinax*, the vessels on the surface of the vitelline sac are brought in close contact with the highly vascular folds which line the oviducts. But in *Carcharias*, as Müller has demonstrated in his Memoir on the subject, not only is there an approximation of the foetal and maternal vessels, but the surfaces of the yolk-sac and of the oviduct are both deeply convoluted, and the projections of the one are admitted into and embraced by the concavities of the other, and the opposing surfaces become adherent even. In both *Spinax* and *Carcharias*, the necessary conditions exist for the reaction of maternal and foetal blood upon each other, as is the case in the Mammalia, but to a much more limited extent.*

* Dr. John Davy has shown, that in *Torpedo* the embryo is nourished at the expense of materials furnished by the parent, since the mature foetus weighs more than twice as much as the egg at the time development commenced. *Philos. Trans. 1834. On the development of the Torpedo.*

II. In the second group those fishes are comprised in which *the gestation is either wholly or in part ovarian*, the last stages only of the process usually occurring in the oviduct. Among the genera included in this division are, *Silurus*,* *Blennius*,† *Anableps*,‡ *Pœcilia*,§ and *Embiotoca*.|| In all of these genera impregnation takes place in the ovary, and, as seems probable, while the ovum is still invested with its original envelopes. In Blenny, Rathké has shown, the ovarian gestation having continued about three weeks, that about the end of September the sac ruptures, and that the embryo is discharged into the central cavity of the ovary, which is in fact the oviduct; here the foetus remains till the beginning of January, when it is born. In Pœcilia the foetus is liberated and escapes into the oviduct towards the end of gestation. Valenciennes has given several details in relation to the development of *Anableps Gronovii*, made for the most part upon specimens in an advanced stage of foetalation, the smallest embryo being more than an inch long. He found only seven or eight foetuses in the so-called uterus of each female, and each of the young was surrounded by a distinct sac, which he regards as simply an enlargement of the original envelope of the ovum. The mature foetus he found to be more than one fourth as long as the parent, and except for the non-development of the ovary, was constituted in every respect like the adult, as regards both its internal and external structure.

For the specimens of *Anableps Gronovii*, upon which the following observations were made, I am indebted to the liberality of Dr. Francis W. Cragin, United States Consul at Paramaribo, in Surinam. Among them were three males and five females, four of which last were in different stages of gestation. The different individuals varied from three and a

* Cuvier et Valenciennes Hist. Nat. des Poissons, T. i. p. 540. 1828.

† Rathké, Mem. sur la Develop. de l'Homme et des Animaux, 2me partie. Leipsic, 1833.

‡ Cuv. and Valenciennes, Hist. Nat. des Poiss. T. xviii. p. 245. Paris, 1846.

§ Duvernoy, Ann. des Sc. Nat. T. I. N. S. p. 313. 1844.

|| Agassiz, Am. Journal of Science. Vol. XVI. Second Series, Nov. 1853.

half to nine and a half inches in length, the females being much longer than the males.

I. The smallest female measured three and a half inches in length, but on careful examination no traces of an ovary were discovered ; its development did not appear to have commenced as yet.

II. The next specimen measured seven inches in length, and the ovary was in a state of gestation ; the foetuses, four or five in number, measured but five-eighths of an inch. The ovary appeared single externally ; was invested with peritoneum, which was supported by a more firm but thin membrane of condensed areolar tissue ; on cutting through this, the interior was found filled with sacs corresponding in number to the foetuses, and united to each other and the ovarian walls by a very loose areolar tissue. They had no communication of any kind with each other. With the aid of the point of a needle the sacs were easily detached and removed entire with the inclosed foetus ; the envelope was much larger than was necessary to hold the embryo, and the space between the two was filled with a fluid, a portion of which (albumen ?) had been coagulated by the action of the alcohol. In each instance it was ascertained that the young had no connection whatever, vascular or otherwise, with the walls of the sac which inclosed it.

The external characters of the embryo, (Pl. 17, Fig. 5,) even at this early stage, as regards its general form and the fins, resemble those of the adult ; but no longitudinal black bands were yet visible on the sides ; the eye had not acquired the prominence of the adult, the cornea was not divided by a transverse band, and the pupil existed in the form of an oval, with its long diameter in a vertical direction, but the sides of the iris had just commenced extending towards the centre in order to form the two laminæ, which, in the adult, give the pupil its singular shape. The umbilical sac forms a spheroidal mass about one fourth of an inch in diameter, and is sufficiently transparent to allow the folds of the intestine which fill

it, to be visible. Externally, the sac is covered with what appear to be parallel projecting lines, extending from the sides of the abdomen to its most prominent part (Figs. 6 & 8.) These Valenciennes describes as "vascular striæ," (*striæ vasculiformes.**) Such was not the nature of these markings in the specimens which I examined; but, when placed under the microscope, were found to form a peculiar structure, which possibly may have some connection with the process of nutrition in their peculiar method of gestation.

The sac itself seemed nearly homogeneous in structure, but the striæ are made up of spherical, or in some cases, pyriform or cylindrical, papillæ or villi, (Fig. 8,) projecting from the surface, and arranged so nearly together in a linear series as to give the appearance of a continuous band. In regard to the minute structure of these papillæ, as far as it could be determined from an alcoholic specimen, they consist externally of an exceedingly thin membrane, inclosing a vast number of minute granules; no vessels were seen in connection with them nor in the membrane to which they were attached. There was no appearance of any communication between the cavity of the papilla and that of the membrane to which it was attached. Within the latter, but more nearly in contact with the intestines, there was a second more delicate membrane, which seemed to be a continuation of the parietal peritoneum. No traces of the yolk were found in connection with the intestines.

III. The third specimen is much longer and measures ten inches in length; the ovary had been ruptured, so that some of the fœtuses had escaped into the cavity of the abdomen, but the whole number of young taken from the parent was much greater than in the preceding case, namely, eighteen; one of these was projecting from the genital opening. They generally resembled the preceding except in size, though the eyes had become more prominent (Fig. 6,) and the iris now

* Op. cit. ex fol. de planche, 539.

exhibited its lateral projections sufficiently developed to give the pupil the shape of a dumb-bell. The umbilical sac has become much larger than in the embryos first described, and measures three eighths of an inch in diameter. The papillæ of the yelk-sac are much more distinct and contain colored granules. The yelk-sac communicates with the cavity of the abdomen by a long fissure extending from a point just behind the union of the opercula nearly as far as the anal opening, consequently beyond the ventral fins. It is from the circumstance just mentioned, doubtless, that an explanation is to be found of the non-union of the ventrals in the adult. The scales terminate abruptly at the edge of the fissure. The intestines, as in the first described embryos, were invested by the internal sac, which was regarded as parietal peritoneum. No bands were visible on the flanks of the body nor were the anal fins yet modified to mark the sexes. A rudimentary liver is visible in these specimens, extending backwards on the left side of the intestinal mass. The intestinal canal is of almost uniform size throughout, there being no distinction between intestine and stomach.

IV. This specimen measured a little less than ten inches in length, but the embryos were of much larger size, having a length of two and a quarter inches; the umbilical sac had disappeared, (Fig. 7,) but the fissure on the under side of the abdomen still remained, and what seems quite remarkable, had grown in dimensions just in proportion to the entire foetus, so that in these specimens it measured one inch in length, and was consequently longer than the whole embryo of the first specimen noticed above. The edges of the fissure were united by the intermedium of a thin membrane, without scales, on which no papillæ were noticed, and was sufficiently lax to allow the edges of the fissure to separate from each other to a slight extent. The transverse band upon the cornea was now distinct, though it had not yet become as opaque as in the adult.

Seven foetuses were found in the ovary; on the sides of

them one or two dark longitudinal lines were now visible ; the general form of the body had assumed more precisely that of the adult, and, as noticed by Valenciennes, the intestines had obtained their permanent form. The external sexual characters were not visible in any of the specimens examined, though they were seen and figured in specimens of about the same size by Valenciennes.

All of the fœtuses of this female had escaped from their original sacs, (no traces of which were now visible,) and were all contained in one large cavity formed by the dilated ovary which now had become analogous to an uterus, and extended from the genital opening as far forwards as the bases of the pectoral fins. The walls of this ovarian sac were sufficiently thin to allow the fœtuses to be seen through them ; on its inner surface, as well as on that of some of the other specimens, were to be seen numerous immature ova, some of them microscopic and others as large as the sixteenth of an inch in diameter. The coexistence of immature ova on the walls of the ovarian cavity, with fœtuses within it, corresponds with what was noticed by Duvernoy in his investigations of the embryology of *Pœcilia*.* The more minute ovarian eggs, though for a long time macerated in alcohol, yet preserved their microscopic characters to a remarkable degree. The smallest consisted of a cell, in the centre of which a nucleus was visible, and around this last were a few granules (Fig. 1) ; in the larger ova the granules have become more and more abundant, and in some instances obscure the nucleus or germ cell. After the egg has increased to a certain size, a clear space (Figs. 2, 3 and 4) appears exterior to the vitelline membrane, which gradually increases to nearly twice the diameter of the egg itself ; this clear space is limited by the substance of the stroma which becomes condensed around it, and thus forms a distinct sac. If the ovum be compared to that of a mammal, then the sac just described may be said

* *Annales des Sc. Naturelles.* T. i. N. S. 1844.

to be analogous to a Graafian vesicle ; that is, the egg of the fish floats free in a sac much larger than itself, just as the mammiferous egg does in the vesicle of De Graaff. There were no intermediate conditions between this and the impregnated condition to enable me to determine whether or not it is this sac which forms the external covering of the foetus. Valenciennes seems to adopt the idea that it does, and compares it to a chorion.* If this view of its nature be true, then there seems no alternative, since development advances so far before the sac ruptures, but to suppose that impregnation must take place through its parietes and that the spermatozoon cannot enter bodily into the substance, or even come in direct contact with the vitelline membrane of the egg, except through the walls of this outer covering, which is not probable. It would seem that it must act simply by its presence on the surface of the egg-sac, or by an endosmosis of its fluid contents through the membranes by which the ovum is invested.

A microscopic examination of the egg-sacs in the advanced foetuses proves conclusively, that they do not consist of loose areolar tissue only, as stated by Valenciennes,† but that while the tissue in question forms the basis of them, they are in reality very highly vascular, large trunks and minute ramifications of vessels being easily traced by the aid of the coagulated blood which they contain.

In comparing foetuses of different stages of development together, a very interesting question is presented to us in connection with their growth. In the smallest specimen examined, the yolk was no longer visible, it had been wholly consumed in supplying materials for the formation of the embryo ; and yet subsequent to this disappearance of the yolk, the embryo, while still in its ovarian sac and cut off from all external communication, continues to increase in size,

* "La cellule qui contient un œuf fécondé s'agrandit et finit par former une sorte de Chorion." Op. cit. T. xviii. p. 261.

† Op. cit. p. 261.

and grows until it acquires the length of an inch and a quarter, which gives the size of the longest fœtus which our specimens furnished. Even the umbilical sac and the fissure which succeeds it, continue to grow after the yolk has disappeared. As a general rule among oviparous fishes, the yolk supplies *all* the material required for the growth of the fœtus; and the same holds good with regard to nearly all Batrachians,* to scaly Reptiles and Birds. So general has this rule been believed to be that none but Mammals have been supposed to contribute any thing beyond the materials of the egg to the support of the young. But recent observations go to prove that some fishes, such as the Torpedo among the Plagiostomes, the Embiotoca among osseous fishes, are to be placed in the same category as Mammals, in relation to the fact of being nourished by the parent during gestation, although neither a placenta is formed nor does any direct vascular communication whatever exist between the fœtus and the maternal circulation. We cannot explain the growth of the fœtal Anableps by any other hypothesis than that it is nourished by a fluid secreted by the walls of the sac in which it is lodged in the earlier stages, or by the parietes of the general ovarian cavity in which the fœtuses are received towards the end of gestation. The high degree of vascular-ity of the egg-sac is favorable to this supposition. As the body of the fœtus, at a very early period, becomes covered with scales, absorption could only take place through the intestinal canal or by the surface of the yolk-sac, which invests the viscera and increases in size for a long period after the yolk itself has wholly disappeared. In the later stages of gestation, even the yolk-sac is out of the question since it in turn wholly disappears, while the fœtus occupies the general cavity of the ovary.

* The only exception among Batrachians, as yet noticed, is found in the Pipæ of South America. See Observations on *Pipa Americana*, by Jeffries Wyman, M. D., in American Journal of Science, 2d Series, Vol. xvii. p. 369.

† Op. cit. Tome xviii. p. 259.

Valenciennes has given a very full and detailed description of the modified ventral fin, which serves the function of an external male organ, and of its connection with the excretory tubes of the testis; yet, in some respects, the specimens which I have examined differ from his description. In these the anal fin (Fig. 9) consisted of two portions, one of which forms a conical-shaped body resting on an enlarged base and attached to or forming the anterior edge of the fin, and is covered with scales as far as its termination; its anterior half is colored black at the base, but the whole of it is so colored nearer the apex; at the extremity is the genito-urinary opening, as described by Valenciennes. Behind the genital portion, and partially imbedded in it, is the true ventral fin, containing seven or eight rays parallel to the genital tube, the posterior being the shortest, and about one half as long as the whole fin. In a larger and adult male, measuring about seven inches in length, the genital portion of the fin has become very much longer and stouter in consequence of the development of muscular fibres in its interior. The genital opening, which, in the preceding specimens, was not at the extremity of the fin, has now become terminal, the fin rays have become proportionally shorter and so closely applied to the posterior face of the genital portion as to be detected with difficulty. In the figure of the fin, given in the *Hist. Nat. des Poissons*, the artist has erroneously represented the fin rays as if they were attached by their base to the side of the genital tube; when in reality they are attached to the under side of the abdomen, and are parallel to the genital tube, but partially imbedded in it.

Valenciennes inclines to the belief that the fin in question could not be used as an intromittent organ in consequence of the scales and fin rays pointing in such a manner as to prove an obstacle. This objection applies less to the adult than the younger specimens, since the fin rays have become much less prominent; but when the structure of the intromittent organ in the males of some Mammals is remembered, as of the

Agouti, where spines projecting in different directions, offer far more serious mechanical opposition, we can readily believe that a structure like that of the anal fin of Anableps may be readily introduced into the genital tube of the female. Still, in the ordinary position of the two sexes it could not be thus used unless bent forwards.

EXPLANATION OF THE FIGURES.

Fig. I. Primitive ova, each consisting of a single nucleated cell.

Figs. II and III. Ova somewhat enlarged, around which a transparent space is formed in the stroma of the ovary.

Fig. IV. A more advanced egg, in which the transparent space has become much enlarged. The vitelline membrane is distinctly visible, and the nucleus contains granules or nucleoli of different sizes. On the left of this figure is an earlier ovum, in which the transparent space is just forming.

Figs. V. and VI. Two fœtuses with yolk-bags attached. On comparing the two figures, which are of the size of nature, it will be seen that fœtus and yolk-bag both grow simultaneously.

Fig. VII. A more advanced and nearly mature fœtus, in which the yolk-bag has been absorbed, and only a linear fissure or umbilicus remains ; this is closed by a thin, scaleless membrane, and extends from the space between the pectoral fins in front to that between the ventrals behind. The fœtus has acquired a length nearly one fourth of that of the adult Anableps.

Fig. VIII. A portion of the yolk-bag, highly magnified, showing the papillæ filled with granules, which cover its surface.

Fig. IX. The anal fin. The genital portion is shorter than the fin rays and membrane. In older specimens, however, the former becomes proportionally longer, and the latter become so much diminished in size as to be scarcely traceable.*

* For complete and accurate descriptions and figures of other details relating to structure and development, reference may be made to the *Hist. Nat. des Poissons*, by Cuvier and Valenciennes, Tome xviii. p. 245.

II.



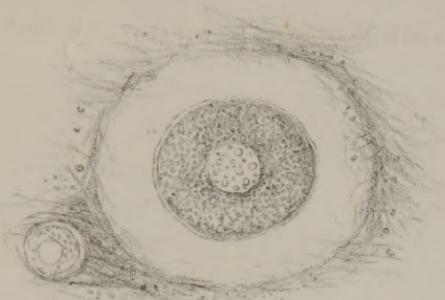
I.



III.



IV.



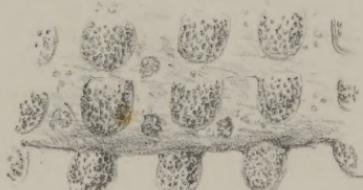
VI.



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VII.



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